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THE EFFECT OF EXTENT OF DISTRIBUTION ON SPECIATION

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WHILE engaged in some research work on the geographic distribution of mammals under the supervision of Professor H. D. Reed at Cornell University in the fall of 1910 and the spring of 1911, certain conceptions regarding the relation between extent of distribution and the generic and specific modifications of mammals were brought to light. Due to the valuable and helpful criticism of Professors C. A. Kofoid and J. C. Merriam, and Dr. J. Grinnell, and of other members of the University of California, and to the advice and aid of Professor C. A. Kofoid, the rather vague ideas then formed have been worked over and crystallized into their form as presented in this paper.

In the past, much of the work that has been done on zoogeography has dealt with a study of the facts of distribution, both present and past, as they stand, together with a study of the factors influencing distribution and speculations regarding the explanation of some of the interesting and apparently anomalous facts thus brought to light. In all of this work, the distribution of animals has been considered almost entirely as the effect of certain biological and geological causes. The present paper is intended to show that the distribution of animals is not only the effect of other causes, but is in itself the cause of other effects, and that extent of distribution has a direct influence on the modification and speciation of the group concerned.

To find out how far-reaching and how potent is this effect, much further study is necessary, not only of the distribution of various groups, but of their classification and systematic relationships as well.

In brief, the effect of extent of distribution on groups of different systematic rank may be stated as follows: As the range of a group of animals, be it genus, family, or order, is extended, the species increase out of proportion to the genera, the genera out of proportion to the families, and the families out of proportion to the orders. In other words, if we assume that in a distributional area of certain extent, there are three genera and six species, in a distributional area of twice that size, there will not be six genera and twelve species, but more probably only four or five genera, and twelve species; *i. e.*, if in the first case the index of modification (a term here used to indicate the average number of species per genus) be two, in the second case it will be greater than two.

As new distributional areas are added, other factors remaining equal, there is a constant increase in number of species and subspecies, going hand in hand with a diminishing rate of increase in genera, the result being a constantly larger index of modification as the area inhabited by a group of animals is extended.

It should be remarked that a unit of area in this connection should be considered a distributional unit, not a geographical unit. In other words, while the addition of one hundred square miles might or might not involve a change in the life of a region, the addition of a new "life zone," "fauna," or association" (see p. 155) would inevitably involve a biotic change, and therefore the addition of one or several of any of these distributional areas should be considered as an addition of a unit, comparable to another unit of similar kind.

Two possible ways of testing this hypothesis present themselves. We may compare the faunas of distributional areas of dissimilar size, or we may compare the specific and generic differentiation found within families occupying areas of different extent. The former method we should expect to work out with a fair degree of accuracy, but the latter involves so many modifying circumstances that even if sufficient data were at hand, it would be difficult to prove anything by it. In the first place there is the difficulty of comparing, in a distributional sense, the areas occupied by different families, since, as pointed out above, the geographic areas do not necessarily coincide at all with distributional areas; in the second place, while it is justifiable to compare the speciation of a family in one region with the speciation of the same family in another region, it is of doubtful value to compare the speciation of one family with that of another in the same or different regions, unless the other factors controlling their speciation be comparable or nearly so. In view of this there are few families which could be advantageously compared with each other as to speciation in relation to extent of distribution, yet in the families which do seem to lend themselves to such a comparison, the evidence all points towards the correctness of the law here proposed.

The bats seem as favorable for such an interfamily comparison as any group of mammals that could be selected, and the table (Table I) of their distribution by

TABLE I

DISTRIBUTION AND SPECIATION OF FAMILIES OF CHIROPTERA

Data Derived from Sclater and Sclater (1899)

Family	Distribution	Gen.	Sp.	Index of Mod.
Vespertilionidæ	Cosmopolitan	17	190	11.18
Emballonuridæ	Warm parts of both hemispheres	15	79	5.27
Pteropodidæ	Old World	18	110	6.11
Rhinolophidæ	Old World	6	61	10.16
Nycteridæ	Warm parts of Old World	2	15	7.50
Phyllostomidæ	Neotropical	36	81	2.25

families is significant. One family, the Vespertilionidæ, is cosmopolitan, inhabiting every zoologic region and *every* life zone, and it has 11.18 species per genus, the highest of any family of bats. The Phyllostomidæ, on the other hand, has the narrowest range, occupying only the warm zones of one zoologic region, namely, the neotropic, and has in 36 genera only 81 species, giving 2.25 as the

TABLE II

DISTRIBUTION AND SPECIATION OF FAMILIES OF INSECTIVORA

Data Derived from Sclater and Sclater (1899)

Family	Distribution	Gen.	Sp.	Index of Mod.
Soricidæ	Palearctic, Ethiopian, Oriental and Nearctic regions, all zones	11	125	11.36
Erinaceidæ	Palearctic, Ethiopian, and Oriental regions	2	16	8.00
Talpidæ	Palearctic and Nearctic regions, temperate zones only	11	25	2.27
Tupaiidæ	Oriental region, warm zones	2	15	7.50
Macroscelidæ	Ethiopian region, warm zones	3	17	5.66
Potamogalidæ	Central Africa and Madagascar, tropical zones	2	3	1.50
Galeopithecidæ	Malay only, forests, tropical zones	1	2	2.00
Chrysochloridæ	South Africa	1	7	7.00
Centetidæ	Madagascar	7	21	3.00
Solenodontidæ	Cuba and Hayti	1	2	2.00

index of modification. The other figures in this table are significant, but the indices of modification in the families Rhinolophidæ and Nycteridæ are abnormally large, and will probably be reduced by subsequent subdivision of genera, or discovery of new forms.

Table II shows the generic and specific differentiation

of the various families of Insectivores, but as some of the families have not been as intensively studied as others, and as the conditions affecting their distribution and speciation are so different in different families, we could hardly expect accurate results, and yet the table clearly shows a tendency for the families having wider ranges to have a higher index of modification, the almost cosmopolitan shrews, for instance, having 11.36 species per genus, and the families with restricted range (Galeopithecidæ, Solenodontidæ, Centetidæ and Potamogalidæ), having only 1 to 3 species per genus. The Talpidæ and Chrysochloridæ do not seem to conform in their speciation to what should be expected.

When the specific and generic subdivisions of all the families of mammals have been worked out more perfectly, and their ranges in a distributional sense, *i. e.,* through life zones, faunas, and associations, are more accurately known, some interesting facts concerning the relation between their indices of modification, and the extent of their ranges, might be brought out.

It is interesting to note that there is a considerable number of conspicuous examples of wide-ranging genera which are remarkably poor in species. Among carnivorous mammals there are many such cases, these animals seeming to be adaptable to an almost unlimited range of environmental conditions without modification, or, in other words, their germ plasm is not stimulated to change by altered conditions of climate or environment. The tiger, for instance, is equally at home in the bleak frozen steppes of Siberia, or in the hot humid jungles of India. The genus *Cynaelurus* is widely distributed over the Ethiopian and Oriental regions, and yet it contains but a single species, with several geographic races. Among birds there are a number of similar examples, the most striking case, perhaps, being *Pandion,* a cosmopolitan genus with but a single species. The same peculiar condition occurs among lower animals, as for instance in the Dinoflagellate genus *Diplopsalis,* which is cosmopolitan

TABLE III*A*

SPECIATION OF MAMMALS IN VARIOUS DISTRIBUTIONAL AREAS IN CALIFORNIA

Data from Grinnell (1913A), (1908), Grinnell and Swarth (1913)

Group	Boreal and Upper Transition Zones					
	San Jac. Mts. (350 Sq. M.)		San Bern. Mts. (550 Sq. M.)		Sierra Range (30,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Ungulata	1	1	1	1	2	4
Bovidæ					1	1
Cervidæ	1	1	1	1	1	3
Antilocapridæ						
Rodentia	7	8	10	12	21	57
Sciuridæ	4	4	5	5	6	22
Castoridæ						
Aplodontidæ					1	1
Muridæ	2	3	3	5	7	17
Geomyidæ	1	1	1	1	1	5
Heteromyidæ			1	1	1	2
Zapodidæ					1	2
Erethizontidæ					1	1
Ochotonidæ					1	3
Leporidæ					2	4
Carnivora	6	6	2 (7)	2 (8)	14	21
Felidæ	2	2	(2)	(2)	2	3
Canidæ	1	1	1 (2)	1 (2)	3	6
Mustelidæ	3	3	1	1	7	10
Procyonidæ			(1)	(1)	1	1
Ursidæ			(1)	(2)	1	1
Insectivora	2	2	2	2	4	11
Soricidæ	1	1	1	1	2	7
Talpidæ	1	1	1	1	2	4
Cheiroptera	2	3	2	3	4	7
Phyllostomidæ						
Vespertilionidæ	2	3	2	3	4	7
Molossidæ						
Total	18	20	17 (22)	20 (26)	45	100
Indices of modification	1.11		1.17 (1.81)		2.22	

in warm and temperate seas, and yet is composed of not more than two species. No adequate explanation of these exceptional cases has been offered, and it is probable that their speciation, or lack of it, is due to conditions of their existence or constitution which we do not understand, or do not recognize.

To test the law by comparison of faunas of areas of different extent, a series of tabular comparisons of the faunas of various regions of different size and character was made. In all of these tabulations, care has been taken in the choice of areas for comparison to make them of unequal size from a distributional point of view, and to make them reasonably comparable. An arctic and a tropical region, for example, are not considered reasonably comparable as regards number of genera and species, nor is a region on the outskirts of the range of a group considered comparable with a region near its center of distribution.

Table III shows a comparison of the mammals of various parts of California. The regions compared are as follows: (*A*) the boreal and transition zones of (*a*) the San Jacinto Mountain range, (*b*) the San Bernardino Mountain range, and (*c*) the entire Sierra range, including the Warner and Shasta Mountains to the north, and the San Bernardinos and San Jacintos to the south; (*B*) a comparison of all the zones of (*a*) the San Jacinto Mountains with the immediately adjoining country, (*b*) the Sierra range as defined above, and including their foothills, and (*c*) the entire state.

A careful study of Table III brings out a number of interesting and significant facts, and bears out the law here proposed with unexpected accuracy, barring one seeming exception which, as we shall see later, can not truly be considered as such.

Let us compare first the three areas in which only the two uppermost life zones are involved, and from which the species invading only the lower Transition zone have also been excluded. First, a word as to the areas compared. The Boreal and Transition zones of the Sierras take in over one half of all the representation of these zones within the whole state. These zones of the San Bernardino and San Jacinto mountain masses are, as compared with the entire range, very small indeed, and comprise almost as small areas as could justifiably be

TABLE IIIB

(*Data as above*)

(*Data as in Table IIIA*)

Group	All Zones					
	San Jac. Mts. (2,500 Sq. M.)		Sierra Range (60,000 Sq. M.)		California (158,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Ungulata	2	2	3	7	4	10
Bovidæ	1	1	1	2	1	2
Cervidæ	1	1	2	5	2	7
Antilocapridæ					1	1
Rodentia	16	41	28	110	31	203
Sciuridæ	5	7	7	26	7	41
Castoridæ					1	2
Aplodontidæ			1	1	1	2
Muridæ	5	14	10	33	11	64
Geomyidæ	1	4	1	9	1	19
Heteromyidæ	3	12	4	24	4	48
Zapodidæ			1	2	1	5
Erethizontidæ			1	1	1	1
Ochotonidæ			1	3	1	3
Leporidæ	2	4	2	11	3	18
Carnivora	9	10	15	29	17	51
Felidæ	2	2	2	3	2	6
Canidæ	3	4	3	9	3	17
Mustelidæ	3	3	7	13	9	22
Procyonidæ	1	1	2	3	2	4
Ursidæ			1	1	1	2
Insectivora	3	3	5	12	6	20
Soricidæ	2	2	3	8	4	14
Talpidæ	1	1	2	4	2	6
Cheiroptera	4	7	7	12	11	26
Phyllostomidæ					1	1
Vespertilionidæ	4	7	6	11	8	21
Molossidæ			1	1	2	4
Total	34	63	58	170	68	310
Indices of modification	1.85		2.93		4.56	

considered to be individual faunal units. The San Jacintos are somewhat smaller than the San Bernardinos, but the difference is almost inconsiderable when compared with the Sierras. Before examining the table, let us see

what conditions in number of genera and species would be expected in these three areas. The San Bernardinos, being almost as small a faunal unit as should be separately considered, we should expect to approach a minimum index of modification, *i. e.,* a minimum number of species per genus, approaching one as a limit. On the San Jacintos, these being smaller than the San Bernardinos, we should expect fewer types according to the law suggested by Grinnell and Swarth (1913), that the number of persistent types in a disconnected area varies directly with the size of the area. On the entire Sierra range we should expect, due to the greatly increased territory, a considerable increase in genera, but a very much greater increase in species. Looking now at Table III, we find that with the single exception of the carnivores on the San Bernardino Mountains, not one discrepancy exists. The Ungulates, Insectivores and bats are represented by the same numbers of genera and species on both of the small areas, and all of them show a marked increase in genera and species on the larger area, in every case with an increase in the index of modification.

The rodents, which show a larger degree of differentiation than any of the other groups, show a very interesting advance in the index of modification as the area is extended. The carnivores, as stated above, show a seeming discrepancy, inasmuch as there are six genera and six species existing on the San Jacintos, and only two genera and two species on the San Bernardinos, whereas, if they conformed with our laws of distribution, we should expect at least six, and possibly seven or eight, species to be found there. On page 35 of Grinnell's "Biota of the San Bernardino Mountains" (1908) we find reference to a number of carnivores now rare or extinct on the San Bernardinos, which undoubtedly have been exterminated by man within the last fifty years. Counting these forms, which it seems to me we are justified in doing, the table bears out the law without a single exception, not only for

the total of mammalian forms, but the totals for each order and for each family.

In comparing the three areas in which all the life zones are involved, the truth of the effect of extended distribution on speciation is still more forcibly impressed upon us. In this case we are comparing areas which are successively larger in size, the San Jacintos, with their foothills and low passes involving the fauna of an area of about 2,500 square miles, the Sierras, about 60,000 square miles, and the whole state of California about 158,000 square miles. The following table, derived from Table III, is very significant in showing the diminishing in-

Group	Genera			Species			Index of Modification		
	San Jac.	Sier.	Cal.	San Jac.	Sier.	Cal.	San Jac.	Sier.	Cal.
Ungulates.....	2	3	4	2	7	10	1.00	2.33	2.50
Rodents.....	16	28	31	41	110	203	2.56	3.93	6.45
Carnivores....	9	15	17	10	29	51	1.11	1.93	3.00
Insectivores...	3	5	6	3	12	20	1.00	2.40	3.33
Cheiroptera...	4	7	11	7	12	26	1.75	1.71	2.36
Totals.....	34	58	68	63	170	310	1.85	2.93	4.56

crease of genera, and the constantly increasing addition of species as the area is enlarged.

By comparing the upper zones of the San Jacintos with the San Jacintos as a whole, and the upper zones of the Sierras with the Sierras as a whole (see Table III), we find that increasing the life zones has in a lesser degree the same effect as increasing the geographic area regardless of zones; in other words, adding life zones tends to have the same effect on speciation as adding faunas and associations without life zones. The following table (derived from Table III) illustrates this:

Mammals	San Jac. (Upper Zones)	San Jac. (All Zones)	Sierras (Upper Zones)	Sierras (All Zones)
Genera.....	18	34	45	58
Species.....	20	63	100	170
Index of mod.....	1.11	1.85	2.22	2.93

Another rough test of the hypothesis was made in a comparison of the mammalian faunas of some of our

large continental islands and zoologic regions, the results being shown in Table IV. The data used in this table are

TABLE IV

SPECIATION OF MAMMALS IN VARIOUS CONTINENTAL ISLANDS AND ZOOLOGIC REGIONS

Data from Sclater and Sclater (1899)

Group	Africa (11,770,000 Sq. M.)		Australian Region (3,390,000 Sq. M.)		Australia (2,947,000 Sq. M.)		New Guinea (312,000 Sq. M.)		Madagascar (228,000 Sq. M.)	
	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.
Ungulates...	155	35							1	1
Rodents.....	196	41	69	8			18	5	13	7
Carnivores...	59	22							9	7
Insectivores..	73	8							20	9
Bats.....	101	19	83	26			39	16	21	12
Lemurs.....	8	3							36	11
Primates....	72	6								
Hyraces.....	14	1								
Elephants...	1	1								
Edentates...	6	2								
Marsupials..			144	36			36	14		
Monotremes.			5	3			3	2		
Totals.....	685	128	301	73	169	59	96	37	100	47
Index of modification...	5.35		4.12		2.86		2.59		2.13	

by no means up to date, being taken from the summaries in Sclater and Sclater (1899), but the subsequent additions to the faunas of the places concerned, and the splitting up of genera and species, have probably been approximately proportionate in each of the five areas, and therefore the figures used are sufficiently accurate to be significant. Comparing Africa, the Australian region, Australia, New Guinea and Madagascar, which rank in size in the order given, we find that the indices of modification of their mammalian faunas are as follows: Africa 5.35, Australian region 4.12, Australia 2.86, New Guinea 2.59, and Madagascar 2.13. Certainly these figures are significant.

Comparing the mammalian faunas of the various islands of the Philippine Archipelago (Table V), we find that there is even here some corroboration of our law of

TABLE V

SPECIATION OF MAMMALS IN ISLANDS OF THE PHILIPPINE ARCHIPELAGO

Data from Hollister (1912)

Island	Sq. Miles	Sp.	Gen.	Index of Mod.
Luzon	40,969	72	40	1.80
Mindanao	36,292	61	32	1.90
Samar	5,031	16	13	1.23
Negros	4,881	14	13	1.07
Panay	4,611	10	8	1.25
Palawan	4,027	21	18	1.16
Mindoro	3,851	17	11	1.54
Leyte	2,722	9	8	1.12
Cebu	1,762	8	7	1.14
Bohol	1,441	3	3	1.00
Masbate	1,236	5	4	1.25

speciation. Considering the large element of chance in the animal population of a group of islands of such small size as those of the Philippines, where the various islets are at a varying distance from each other, and their faunas have originated from different sources, the relation between their size and the differentiation of their forms is remarkably regular. In Table V, where the main islands have been listed in order of size, with their numbers of genera and species of mammals, the deer have been excluded entirely, since their generic and specific differentiation is in too chaotic a state to be used. The most striking fact brought out by the table is the lead which the two large islands, Luzon and Mindanao, show, not only in total number of forms, but in index of modification as well. With the possible exception of Mindoro and Palawan, practically none of the smaller islands is supporting as large a variety of mammalian forms as could be expected of it, a fact which might be explained in a number of ways.

In all of the tabulations given, the marine mammals have been entirely excluded since the factors affecting their distribution and speciation are so different from those of terrestrial mammals. In the majority of cases marine mammalian families have a paucity both of genera and species, a circumstance brought about by a number of factors. Generally speaking, large, wide-ranging

forms, or forms which are poor in numbers of individuals, are poor in genera and species, possibly due to the comparative uniformity of their environment, which is usually coincident. Most marine mammals are of these kinds, and their paucity of types is emphasized by the comparative uniformity of their environment, even in the most widespread groups. From a distributional point of view, *i. e.,* taking into account life zones, faunas and associations, a cosmopolitan, oceanic, surface group of animals does not range through as great a variety of ecologic niches and environmental and climatic conditions as does a cosmopolitan terrestrial group.

In order to determine whether the principles of distribution and differentiation here set forth would apply to birds as well as to mammals, a number of series of comparisons was made as with mammals, and with exactly comparable results.

TABLE VI

SPECIATION OF BIRDS IN VARIOUS CALIFORNIA AREAS

Data from Grinnell (1913B), (1908), Willett (1912)

Group	San Bernardino Mts. (2,000 Sq. M.)		Southern California (30,000 Sq. M.)		California (158,000 Sq. M.)	
	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.
Passeres	62	82	79	114	87	197
Picariæ	16	20	19	23	20	38
Striges	3	3	7	7	8	15
Accipitres	5	5	10	14	12	17
Columbæ	1	1	2	2	3	3
Galli	1	1	3	3	6	11
Limicolæ	3	3	4	4	9	10
Grues	1	1	5	6	6	8
Waders	2	2	7	7	8	11
Anseres	2	2	5	5	11	11
Other water birds	1	1	12	14	16	26
Total	97	121	153	199	186	347
Index of mod.	1.25		1.30		1.87	

Table VI gives a comparison of genera and species of resident birds of (*a*) the San Bernardino Mountain region, (*b*) Southern California, and (*c*) California as a whole. Almost without exception, in each individual group of birds there is a reduction in the index of modi-

fication as the area is restricted from California to the Pacific Coast region of Southern California, and finally to the San Bernardino region. The totals reflect the trend in each group. While in the largest area the number of genera is considerably less than double what it is in the smallest, the number of species is more nearly tripled. The Southern California area is intermediate.

TABLE VII

SPECIATION OF RESIDENT BIRDS IN AUSTRALIA AND TASMANIA

Data from North (1901–1909)

Group	Australia (2,947,000 Sq. M.)			Tasmania (26,000 Sq. M.)		
	Sp.	Gen.	Fam.	Sp.	Gen.	Fam.
Passeres	304	119	26	53	42	15
Picariæ	29	18	6	7	7	3
Striges	9	2	2	1	1	1
Accipitres	27	17	2	11	9	2
Psittaci	57	14	3	11	9	3
Total	426	170	39	83	68	24
Index of generic mod.		4.35			2.83	
Index of specific mod.	2.30			1.22		

Table VII shows a comparison of the families, genera, and species of resident birds of Australia and Tasmania, from North (1901–1909). Here again, in addition to a very marked diminution of the total number of types in Tasmania as compared with Australia, each group shows a considerable decrease in the ratio of genera to families, namely, from 4.35 in Australia to 2.83 in Tasmania, and of species, to genera going from 2.30 in Australia to 1.22 in Tasmania.

Table VIII is a similar comparison of (*a*) the resident birds of Ireland, from Hartert (1912), (*b*) the resident birds of all the British Isles, from Hartert (1912), (*c*) all the species of the Palaearctic region, the great majority of which are resident in one part or another, from Dresser (1902), (*d*) all the species of Japan, many of which are not resident, from Ogawa (1908), and (*e*) all the species of Kamtschatka, where the majority are resident, from

TABLE VIII

SPECIATION OF BIRDS IN VARIOUS PALEARCTIC REGIONS

Data from Hartert (1912), Dresser (1902), Ogawa (1908) and Stejneger (1885)

Group	Ireland (32,583 Sq. M.)		British Isles (120,900 Sq. M.)		Palearctic Region (19,150,000 Sq. M.)		Japan (147,700 Sq. M.)		Kamtschatka (105,000 Sq. M.)	
	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.	Sp.	Gen.
Passeres	57	35	85	42	610	116	180	64	55	38
Picariæ	4	4	7	7	81	21	34	16	8	5
Striges	2	2	5	4	34	11	14	8	4	3
Accipitres	7	4	12	7	66	21	23	14	15	7
Columbæ	4	2	4	2	29	6	12	6	0	0
Galli	4	4	8	7	76	19	11	5	5	3
Limicolæ	10	9	15	11	97	32	45	21	25	17
Grues	4	4	5	5	34	13	27	9	1	1
Waders	1	1	1	1	31	12	23	12	0	0
Anseres	8	8	16	12	64	24	39	21	28	20
Other water birds	23	14	30	15	129	35	83	28	32	18
Total	124	87	188	113	1,251	310	491	204	183	112
Index of mod.	1.42		1.66		4.00		2.40		1.63	

Stejneger (1885). The increase in index of modification from Ireland to the British Isles, and then to the entire Palaearctic region, is almost exactly what should be expected. The greater number of both genera and species in Japan as compared with Kamtschatka reflects the greater variety of ecologic niches in a warm country as compared with a cold one of comparable size. A comparison of the *resident* species of Japan with the resident species of the British Isles would be of very great interest, but such a list of Japanese birds is not available. The very striking similarity between the speciation of birds in Kamtschatka, and that in the British Isles, both in number of genera and of species, is very remarkable. The interesting manner in which the balance of nature is preserved is shown by the large representation of raptorial birds to parallel the abundance of shore birds and Anseres.

That reptiles and amphibians are influenced in their speciation by their distribution is indicated by Table IX, which shows a comparison of the genera and species of amphibians, lizards, and snakes, in three of the geographic areas defined by Cope (1898).

TABLE IX

SPECIATION OF AMPHIBIA AND REPTILIA IN NORTH AMERICAN AREAS

Data from Cope (1889), (1898)

Group	Lower California District (12,000 Sq. M.)			Western Sub-region (500,000 Sq. M.)			Medicolumbian Region (4,500,000 Sq. M.)		
	Sp.	Gen.	Index of Mod.	Sp.	Gen.	Index of Mod.	Sp.	Gen.	Index of Mod.
Amphibia.....	4	3	1.25	23	10	2.30	130	28	4.64
Lacertilia.....	17	13	1.30	28	13	2.15	143	31	4.61
Ophidia.....	16	12	1.33	20	9	2.22	191	45	4.24

The "Lower California district" consists of only the tip of Lower California; the "Western subregion" embraces the Pacific slope of North America from Northern Mexico, east of the Sierras, to Oregon, where it crosses the Sierras to the Rocky Mountains, including northern Idaho, eastern Montana, and most of British Columbia. The "Medicolumbian region" includes northern and central Mexico, and most of the United States and Canada north to a line drawn diagonally from New England to Alaska, interdigitating on its border with the "Holarctic region."

The almost exactly parallel increase in the indices of modification in the three groups of cold-blooded vertebrates considered, as the area is extended, is quite remarkable. All three groups average from 1.25 to 1.33 species per genus in the smallest area, from 2.15 to 2.30 in the intermediate area, and from 4.24 to 4.64 in the largest area.

As suggested by Professor Kofoid, a factor influencing speciation in such diverse vertebrates as mammals, birds, reptiles, and amphibians, should be very widely applicable to speciation in the entire animal kingdom.

A series of statistics relating to various orders of insects and other invertebrates has been compiled to ascertain whether in these groups as well as in vertebrates, the number of species increases out of proportion to the genera, as the size of the area, in a distributional sense, is enlarged.

TABLE X

SPECIATION OF ELATERIDÆ IN VARIOUS AREAS OF UNEQUAL SIZE

Data from Schwarz (1906)

Region	Sq. Miles	Sp.	Gen.	Index of Mod.
Africa	11,770,000	574	55	10.43
Madagascar	228,000	245	36	6.80
India	1,760,000	438	53	8.26
Borneo	296,700	150	40	3.75
Sumatra	184,000	177	41	4.31
Java	50,000	125	35	3.37
Ceylon	25,333	96	28	3.42
Australia	2,947,000	386	42	9.19
New Guinea	312,000	61	20	3.05
New Zealand	104,750	137	24	5.70
Tasmania	26,000	13	7	1.86

Table X was compiled to show the number of genera and species of beetles of the family Elateridæ in various continents and islands, the regions chosen for comparison being well defined areas of unequal size.

A careful inspection of this table shows that with only two exceptions the indices of modification are directly proportional to the size of the areas. Borneo and New Guinea, however, not only show a smaller index of modification than should be expected of them, but are poor in total number of types. Nevertheless, when we reflect that these two islands are not nearly so thoroughly known to science as are the other areas considered in the table, no great significance can be attached to their seeming paucity of known types.

Table XI shows the number of genera and species of Limnophilidæ, a family of Trichoptera, in eastern North America (east of the Rockies) as compared with North America as a whole. It will be noticed that while in the

TABLE XI

SPECIATION OF LIMNOPHILIDÆ (TRICHOPTERA) IN NORTH AMERICA

Data from Ulmer (1907)

Region	Sq. Miles	Sp.	Gen.	Index of Mod.
North America	8,000,000	98	27	3.63
Eastern North America	5,000,000	45	20	2.25

larger area the number of species is more than double what it is in the smaller area, the increase in genera is only about one third, increasing the index of modification from 2.25 to 3.63.

Table XII shows practically the same thing in the case of the hawk moths of the family Sphingidæ.

TABLE XII

SPECIATION OF SPHINGIDÆ IN AMERICAN AND AFRICAN AREAS

Data from de Rothschild and Jordan (1907)

Area	Sq. Miles	Sp.	Gen.	Index of Mod.
West Indies	76,000	61	20	3.05
Mexico and Central America	975,200	122	34	3.58
South America	7,000,000	197	35	5.62
Mex., Cent. Am., and S. Am.	7,975,200	237	40	5.92
Mex., Cent. Am., S. Am., and W. I.	8,051,200	262	41	6.39
Bourbon	965	7	5	1.40
Madagascar	228,000	39	20	1.95
Africa	11,772,000	166	48	3.45
Africa and Mad.	12,000,000	195	53	3.67
Africa, Mad., and Bourbon	12,000,965	197	53	3.71

In this case two series of tabulations were made, one showing the number of genera and species in various Neotropical areas, and combinations of these areas, the other showing a similar tabulation for various Ethiopian areas, with similar combinations. It will be observed that the speciation in the West Indies is very large for the size of the area involved, but when we consider the abundant opportunity that has been given for isolation to operate, this is not surprising. The index of modification is quite low. Mexico and Central America have a larger speciation, compared with South America, than would normally be expected, the reason being that Central America is the American center of distribution. The index of modification, however, reflects the smaller size of the area, being considerably lower than that for South America. The increase in index of modification from 5.62 to 6.39, as areas are successively added to South America, is significant. Looking now at the Ethiopian regions, we find that there is the same disproportionate increase of species over

genera in successively larger areas, the index of modification increasing from 1.40 in the small island of Bourbon to 1.95 in Madagascar, and 3.45 in Africa. Combining Africa and Madagascar, this is increased to 3.67, and with the island of Bourbon, to 3.71.

Table XIII is one of especial interest, since it deals

TABLE XIII

SPECIATION OF MARINE GAMMARIDEA (AMPHIPODA) IN VARIOUS SEAS

Data from Stebbing (1906)

Area	Sp.	Gen.	Index of Mod.
Mediterranean Sea	147	67	2.19
Arctic Ocean	311	140	2.22
N. Atlantic Ocean	475	176	2.70
S. Atlantic Ocean	65	44	1.47
Arctic and N. Atlantic	588	191	3.07
Arctic, N. Atlantic, and S. Atlantic	645	207	3.11
Arctic, N. Atlantic, S. Atlantic and Med. Sea	735	214	3.43
Whole family	1,333	313	4.22

with a marine instead of a terrestrial group. It embodies the results of a compilation of the marine genera and species of Amphipoda of the suborder Gammaridea in a number of the oceans and seas of the world. Since it is primarily a cold-loving group, the largest numbers are found in the cold seas, the Arctic and North Atlantic being the home of considerably over half of the known marine species. It is very likely that when the Antarctic regions have been studied as thoroughly as the northern regions, the number of species from that part of the world will be very considerably increased. At the time of Stebbing's work on Amphipoda, our knowledge of Antarctic and contiguous areas was very meager.

The steady increase of the index of modification from the smaller to the larger seas is striking. The Mediterranean Sea, although it is the most thoroughly known of all, has the lowest index of modification, namely 2.19, the Arctic Ocean comes next with 2.22, and then the North Atlantic with 2.70. The small number of species from the South Atlantic and Antarctic regions has already been

mentioned, and its low index of modification may be attributed to the same sort of imperfect knowledge as in the case of Borneo and New Guinea in Table X. The constant growth of the number of species per genus from 2.22 to 3.43 as the various seas and oceans are added together, exactly parallels the results obtained in a similar way for a terrestrial group in Table XII. The comparison of the speciation of the largest area for which it was worked out, with the speciation of the entire group, many species and genera of which inhabit fresh water, is interesting, jumping as it does from 3.43 to 4.22. From the facts brought to light by this table it can hardly be doubted that practically the same influence is brought to bear on the speciation of marine as on terrestrial organisms by the extent of their distribution.

The theoretical explanation here proposed for this phenomenon involves a number of complex problems relating to evolution and speciation, including isolation, effect of time, causes of specific and generic modification, etc., each of which will be dealt with in the following pages as they seem to influence the law here proposed.

Let us first consider the factor of isolation in relation to the production of new forms. As excellently stated by Cook (1909), isolation can not be considered as a cause or factor in evolution, since changes in the characters of species are not dependent upon the subdivision of species to form additional species. To quote from him:

> The separation of species into two or more parts allows the parts to become different, but there is every reason to believe that evolutionary changes of the same kind would take place if the species were not divided. That the isolated groups become different, does not indicate that isolation assists in the process of change. It gives the contrary indication that changes are restricted by isolation. If isolation did not confine the new characters to the group in which they arise, the groups would remain alike, instead of becoming different. . . . Isolation is the shears that splits the species, not the loom that weaves it.

Therefore, while isolation can not be considered a factor in evolution, it is an important factor in speciation. Species vary in many directions or orthogenetically pro-

gress in a definite direction, but the trend of variation or progression may be different in one locality, and tend towards a different result, from that of another locality. Whether the evolution, usually in more or less divergent directions, of segregated groups of individuals be looked upon (1) as the accumulation of numerous slight variations which have a different average character in any two portions of a species, as originally explained by Darwin (1859, Chap. 4) or (2) purely as the result of natural selection, as argued by Wallace (1858), or (3) as the result of a change in the average character of two portions due to the uneven occurrence of mutations in the two portions, a conclusion reached by Dewar and Finn (1909, p. 380), or (4) as the result of orthogenetic evolutionary tendencies inherent in the species and influenced by the environment, as Eimer suggested (1897, Chap. 1), does not concern us here,—the general tendency appears to be that two isolated portions of a species as a general rule trend in different directions, and diverge farther and farther as long as they are isolated.

It is assumed that the greater the length of time given for the influence of isolation to be felt, the farther apart are the two originally identical divisions likely to trend, however the dissimilar evolution be interpreted. As stated by Tower (1906), in speaking of the method of evolution of the Chrysomelid genus *Leptinotarsa,*

> We can interpret the conditions found by any of the current hypotheses; but explaining a condition by an hypothesis is not the same as that the conditions found are evidence in support of an hypothesis, although it is often so used.

The existence of distinct variations, subspecies, and ultimately species and genera, in isolated areas is a too frequently observed phenomenon to be looked upon as anything else than a self-evident truth, but that this should necessarily be considered as supporting any particular theory of evolution can not be argued.

The profound results of prolonged isolation may be observed in the fauna of some of our long-separated con-

tinental islands, such as Madagascar, Australia and New Zealand. Decreasing degrees of isolation may be observed in our West Indian islands, where some generic differentiation has occurred; in the Santa Barbara islands, where there has been a differentiation of species; and the detached mountain ranges of Southern California, where the upper life zones are at present in an isolated condition, but have been so only long enough to develop a few new subspecies, and to lose many of the types of the mother range, in accordance with the law proposed by Grinnell and Swarth (1913) that "the smaller the disconnected area of a given zone, or distributional area of any other rank, the fewer the types which are persistent therein."

From this it is apparent that the time element, in conjunction with isolation, may have a very decided effect on the number of genera and species in a family, but since, from a geologic point of view, animals appear to have reached a new equilibrium very quickly after a geographic change, the time element may have little effect on the numbers of genera and species relative to each other in any given area. In other words, as fast as new genera are produced in a given area, the species within the genera will tend to be produced in the same ratio, thus leaving the index of modification unaffected.

As an example of the effect of time and isolation let us take a hypothetical case. Let us assume that a certain island became divided into two islands of unequal size, and that after a short period of segregation, just long enough for the fauna to readjust itself to the smaller areas and reach a new equilibrium, we had say six species in three genera on the larger island, and three of the same species in two of the genera on the smaller one. After a long period of isolation we should have approximately the same number of genera and species on the two islands, but they would have diverged to generic differentiation. In other words, the effect of time in conjunction with isolation is to increase the number of genera and species in the family, while the index of modification undergoes little change.

This leads us to a consideration of the factors involved in the differentiation of genera as contrasted with the differentiation of species. In general it may be said that extrinsic modifications, *i. e.,* those which are in some way connected with changes in temperature, humidity, character of flora, food, and other environmental conditions, and which usually affect such characters as color, size, length of hair, etc., lead to differentiation of species and subspecies primarily. On the other hand, intrinsic modifications, *i. e.,* those which are related directly or indirectly to a change in the habits or mode of life of the animal or the occupation of a new niche in nature, usually, if not always, lead to generic or family differentiation, since it is evident that changes fitting an animal to live arboreally instead of terrestrially, for instance, are of such a nature, that if they are perpetuated and carried to perfection, will not stop at specific difference but will become of generic importance.

It might be argued that there are no modifications which might not, if carried far enough, ultimately lead to generic differentiation. This is possible, but very improbable, because the modifications here alluded to as "extrinsic" are of such a nature that in the varying climatic conditions there are likely to be intermediate forms which make the division of the more widely separated ones into genera impracticable. In the case of our "intrinsic" modifications, intermediate forms are not so likely to exist when once the incipient changes leading to an altered mode of life have reached a fair degree of perfection.

As a concrete example of what is meant by extrinsic and intrinsic modifications, let us take the squirrels of a given region, say eastern North America. There are four genera to be distinguished,—*Sciurius, Tamias, Sciuropterus* and *Arctomys.* The genus *Sciurus* contains strictly arboreal, mostly nut-eating, omnivorous forms. *Tamias* includes forms which are terrestrial, diurnal, dwelling in natural or artificial holes and crevices, and with a device for carrying food in their cheeks. *Sciuro-*

pterus is an arboreal type which is nocturnal, and has developed characters which enable it more easily to travel from tree to tree. *Arctomys* is the most highly modified form, and has departed most widely in its habits; it is entirely terrestrial, seeks shelter in artificial burrows, eats grass, and hibernates.

Were we to study the characters separating these genera, we should find that they are all characters which enable the animal best to occupy the ecologic niche it fills. If now we select any one of these genera and examine its species, we perceive that the differences we find are not such as could clearly be related to differences in mode of life or habits, but rather such differences as are induced by the circumstances mentioned above, such differences being size, color, length of feet and tail, texture of fur, etc.—*i. e.*, extrinsic variations.

An interesting example of both extrinsic and intrinsic modifications in an incipient stage may be found in the song-sparrows of western United States. Let us compare the form of the humid northwest coast belt, *Melospiza melodia morphna,* with the form of the arid Arizona deserts, *M. m. fallax.* The differences to be observed in color and size are very noticeable, and would undoubtedly lead to their separation into two distinct species were it not for the complete chain of intermediate forms. But even if the chain of intermediate forms were not complete, and after a period of segregation the numerous intergrading subspecies became broken up into a few well-marked species, nevertheless, unless a change in mode of life of the bird were involved, however far the extremes of color and size might tend, they could not be given generic distinction because of the intermediate forms, inhabiting semi-arid or semi-humid regions, which would be almost certain to exist. It hapens, however, that *Melospiza melodia morphna,* and *M. m. fallax,* do differ considerably in mode of life, the former being a beach comber, the latter a nomad of the desert. It would be expected, therefore, that if these two subspecies were isolated, the modifications re-

lated to their difference in mode of life, already shown in an incipient manner, would soon lead to their generic differentiation.

It is not argued that under a given set of ecologic conditions, only one type could be produced, nor that according to the idea of some zoologists, as set forth and refuted by Grinnell and Swarth (1913), should individuals of one geographic race be transplanted into the region of a different geographic race, the first race would assume within a few generations all the characters of the second race. Whether the changes due to the influence of the environment be looked upon as the results of natural selection and adaptation, or merely as the results of a stimulus to the germ plasm, the new type would not necessarily be always the same, this, however, depending upon the number of potential responses in the type, and, as excellently shown by Ruthven (1909) in his study of evolution in the genus *Thamnophis,* upon the modifications previously undergone by the type we are dealing with.

It is very evident that there are many variations in animals which seem to fall into neither the extrinsic nor intrinsic category, but which are neutral and vary independently of climate or habits, and may be inherited phylogenetic tendencies. It is very largely due to these neutral variations, frequently to be ascribed to orthogenetic evolution, tending in different directions in different places, and given an opportunity to diverge by isolation, that different species may be produced to occupy regions of similar climatic and environmental conditions, and different genera may be found occupying the same ecologic niches.

To choose an example in the same family quoted before, we may cite the case of *Tamias* in eastern North America, and *Eutamias* in western North America. In this case the characters separating the genera are not clearly related to their mode of life, the chief difference being the loss of one small premolar in *Tamias,* and its retention in *Eutamias.* The extent of divergence of these neutral varia-

tions depends on the duration of *geographic* segregation, and may therefore be of specific, generic, family, or ordinal rank.

To sum up, specific modifications may be of three kinds: (1) extrinsic modifications, induced by changes of climate and environmental conditions; (2) neutral modifications, due to a different trend of evolution in segregated regions; (3) incipient generic modifications. On the other hand, generic modification may be either intrinsic modifications, concomitant with changes in mode of life or habits of the animal, or neutral modifications as above, given generic value by a longer period of segregation.

Having dwelt for some length on these preliminary considerations, let us now apply them to the case in hand and see how they affect differentiation into species and genera through extension of range.

It is a well-known biological fact that different types of a group of animals, at least of higher animals, are found associated with different environments; nearly related species do not, as a rule, live comfortably together in the same environment, and nearly related genera do not occupy the same ecologic niche in a given zoogeographical area. This does not seem to hold true for animals of lower organization, as conclusively shown by Kofoid (1907). It is common for a group of animals, unless hindered by an impassable barrier or unfavorable environmental conditions, not only to continually extend its range into new territory, but also to attempt to live in as many different niches in nature as possible within a given area. Such attempts to invade new ecologic niches are frequently concomitant with heritable modifications better fitting them to occupy their new situation, though it is difficult to say whether these modifications are causes or results of the change in mode of life. However this may be looked upon, the tendency to occupy new niches in nature is frequently accompanied by intrinsic modifications, and therefore by generic differentiation.

From this we may safely assume that in a given area

a family of animals, by adaptive evolution, will approach a maximum of generic differentiation which can be supported in that area. In other words, every suitable ecologic niche which is represented in the region considered will be invaded by the family, and even in a small area there is likely to be a considerable generic differentiation, especially if isolation has had any opportunity to operate within the area, in breaking up the genera and species.

Let us assume that in one unit of area a certain family, Sciuridae for example, was represented by three genera, each with three species. Second, let us assume that this family kept spreading into additional units of area. With each new unit, the chance of new suitable ecologic niches being represented would decrease, and therefore the chance of new genera being represented would decrease, since if a genus were fitted for its niche in nature under certain conditions of climate and environment, it would in the majority of cases not be likely to undergo any radical changes in the occupation of the same niche under somewhat altered conditions of climate and environment; *i. e.,* the stimulus for intrinsic modification would be lacking.

On the other hand, with each additional unit of area, the chances of the combined conditions of temperature, humidity, and environment being different, would remain the same. In other words, the chances of the three dimensions influencing the life of a region, *i. e.,* "life zone" (controlled by temperature), "fauna" (controlled by humidity), and "association" (controlled by the effect of the other two plus a number of other environmental conditions), intersecting at the same point would be almost equally improbable with each succeeding unit of area. Since it is changes in "life zone," "fauna," or "association" which produce extrinsic changes, and therefore lead to differentiation of species and subspecies primarily, the increment of species would average nearly the same for each succeeding unit of area, other factors remaining equal. It should also be taken into consideration that

with the invasion of new zoogeographic areas, contact with allied forms is frequently experienced, and opportunity is thus afforded for cross breeding and hybridization, the result of which upon the germ plasm appears to be as influential in the production of new forms as is the shock of new environmental conditions. The constant increase in species and subspecies accompanying invasion of new territory, going hand in hand with a diminishing increase in genera, results in the constantly larger index of modification as the area inhabited by a group is extended.

SUMMARY

1. Extent of distribution has a direct influence on the speciation of the group concerned in this way, that as the range of a group of animals is extended, the species increase out of proportion to the genera, the genera out of proportion to the famliies, and the families out of proportion to the orders.

2. Comparison of different families having unequal geographic ranges is usually inaccurate due to the great differences in the other factors controlling their speciation. Those families which do lend themselves to such a comparison show decidedly the effect of extent of distribution, *e. g.*, the bats and some of the insectivores, the families of widest distribution having the largest indices of modification. A number of exceptions exist in the form of certain wide ranging genera which have a paucity of species. We have no adequate explanation for this phenomenon.

3. Comparison of the faunas of areas of different size gives very accurate results. A number of tabulations show as a whole an invariable increase in the index of modification as the distributional area is extended by the addition of either life zones, faunas, or associations. Such tabular comparisons were made for all the classes of terrestrial vertebrates, for several families of insects, and for the marine Amphipoda of the suborder Gammaridea. Allowing for explicable exceptions, the increase in number

of lower systematic groups out of proportion to the increase of higher systematic groups as the area considered is enlarged is a remarkably constant and wide-spread phenomenon.

4. The theoretical explanation here proposed for this phenomenon involves a number of complex problems relating to evolution and speciation, including isolation, the time element, and causes of specific and generic modification.

5. Isolation is an important factor in speciation, since the separation of species into two or more parts allows the parts to become different. The degree of divergence of the segregated parts is largely dependent upon the duration of segregation.

6. Time, in conjunction with isolation and evolution, tends to increase the number of genera and species in a family, but the index of modification, *i. e.,* the average number of species per genus, remains approximately the same in a given area.

7. Three types of modifications in animals may be named:—first, "extrinsic" modifications, which are induced by climate and other environmental conditions, and which lead to differentiation of species and subspecies primarily; second, "intrinsic" modifications, which are concomitant with a change in habits or mode of life of the animal, due to the occupation of a new ecologic niche, and which usually lead to generic or family differentiation; and third, neutral modifications, which are merely the result of the natural tendency of all animals to vary and to be subject to more or less orthogenetic evolution,—modifications which can not be correlated with environmental conditions, nor with a change in mode of life of the animal, but which may be influenced largely by inherited tendencies. Such modifications are responsible for the production, through isolation, of different species to live under the same climatic and environmental conditions, and of different genera to occupy the same ecologic niche.

8. Specific modifications may be of three kinds: (1) ex-

trinsic modifications, (2) neutral variations in segregated regions, (3) incipient generic modifications. Generic modifications may be (1) intrinsic modifications, or (2) neutral varations, given generic value by a longer period of segregation.

9. Since different types of a group of animals are usually found associated with different environmental conditions or different ecologic niches, and since it is common for animals, if unhindered, not only to extend their range continually into new territory, but also to occupy new ecologic niches, and since these tendencies lead to specific and generic differentiations, respectively, any given area will have a differentiation of species proportionate to its variety of environmental conditions, and of genera proportionate to its variety of suitable ecologic niches.

10. Since, as the area of distribution is extended, the chance of new conditions of climate and environment being represented remains approximately the same, the increase in number of species is nearly proportional to the increase in the area of distribution, but since the chance of new ecologic niches being represented in most cases constantly decreases, the increase in genera proceeds at an ever-diminishing rate. This, going hand in hand with the nearly constant increase in species or subspecies, results in a constantly increasing index of modification.

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BIOLOGY OF THE THYSANOPTERA[1]

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I. FACTORS GOVERNING LOCAL DISTRIBUTION

INTRODUCTION

THE Thysanoptera, commonly called thrips, are only beginning to be known, in this country, by systematic entomologists. The systematic knowledge is mostly contained in the monograph of Hinds (1902), a more recent synopsis by Moulton (1911), and a few other papers dealing with new species and with relationships, prominent among which is the work of Jones (1912). Biologically the group is still less known. A considerable number of papers have been issued from experiment stations, describing the life history (egg, larval, pupal and adult stages) and habits of thrips of economic importance. Besides these the principal recent work of a biological nature is a paper of my own (Shull, 1911), on the ecology, method of locomotion, mode of reproduction, and dissemination. The life cycle of most species is still largely unknown.

The first section of this paper is an attempt to carry into further detail the study of the ecology of the Thysanoptera. The first ecological scheme, so far as I am aware, worked out for the Thysanoptera was that of Jordan (1888), who divided thrips into three classes: first, the flower-dwellers; second, the leaf-dwellers; and third, all other thrips (for example, those living on fungi, under wet leaves, under bark of trees, on roots, on lichens, etc.). The inadequacy of this classification, and the difficulty of applying schemes of ecology adapted to other groups of insects, was pointed out in my earlier paper, where I pro-

[1] Contributions from the Zoological Laboratory of the University of Michigan, No. 142 (Biological Station Series, Zoological Publication, No. 10).

posed a new scheme, based on my observations in the field. In this scheme, Thysanoptera were divided into two groups: (1) interstitial species, those living in closely concealed situations, as among the florets of composite flowers, or in clusters of young leaves; and (2) superficial species, those living on exposed surfaces, for example, the surface of leaves. The interstitial species were further divided into an anthophilous division (flower-dwellers) and a phlœophilous division (those living under bark scales on trees). The superficial species were either poephilous (on grass) or phyllophilous (on leaves of plants other than grasses). The distinction between poephilous and phyllophilous seemed warranted, since grass-dwellers were found on many different grasses, but rarely on other kinds of leaves.

Such a classification undoubtedly describes the facts, but does not explain why the habitats named are the ones chosen(?). The factors determining habitat were believed by me at that time to be character of food, and protection afforded. In some species one of these factors predominated, in other species the other factor, while others may have been influenced largely by both. In the light of recent ecological studies, however, the explanation of local distribution in terms of such general environmental factors seems inadequate. Largely owing to the work of Shelford (1911) upon the tiger-beetles, much emphasis is now being placed upon the ecological importance of physiological factors. With a view to relating the distribution of Thysanoptera to the physiology (more specificially, behavior) of the various species, and thus explaining that distribution in more definite terms, the experiments and observations recorded in this paper were made.

This work was done largely at the University of Michigan Biological Station, at Douglas Lake, Michigan, supplemented by observations at Ann Arbor, Michigan, in Ohio and elsewhere.

Facts to be Explained

The following are some of the facts of habits and distribution of the more abundant species for which physiological explanations were sought. Some of these facts are stated in my former paper, some of them doubtless the common property of all thysanopterists; others, so far as I know, have never been recorded.

Euthrips tritici is found almost exclusively *in situations where it is concealed,* as among the florets of composite flowers, in clusters of young leaves, or in almost any close crevice where the tissues are not too hard or tough to be pierced. It appears to make little difference what species of plant is inhabited, provided a concealed situation is available. In the paper cited above (Shull, 1911) I gave a list of seventy species of plant on which *Euthrips tritici* was taken, and I have since collected it on a number of plants not included in that list. But with rare exceptions, it has been found in crevices where it was not readily visible. In related plants, it is always more abundant in those affording concealed situations. Thus, in white clover (*Trifolium repens*) and in red clover (*T. pratense*), this thrips is usually abundant; while on the related yellow, and white, sweet clovers (*Melilotus officinalis* and *M. alba,* respectively), growing along with the red and white clovers, *Euthrips tritici* is usually rare or wanting. The flowers of *Melilotus* are widely separated from one another on the stem, and do not afford concealment (Shull, 1911).

If, while *Euthrips* is in one of these crevices, it is disturbed, as by gently rubbing or pressing the flower, it quickly *comes out of its retreat and crawls rapidly away, or takes to flight.* The larvæ show the same behavior as the adults in this regard, except, of course, that they do not fly.

Anaphothrips striatus is found *usually on grasses* of various kinds, rarely on leaves of other plants. The species of grass seems to make little difference. *Some individuals are found in perfectly exposed situations,* as on

the upper side of grass blades, *others more or less concealed* in the rolled up young leaves (Shull, 1911). I have found, however, that among the adults, *those in exposed situations are almost exclusively females, while those in the rolled young leaves are either males or females.* (For the first time on record, the males of this species, as will be shown in the second part of this paper, have been found in considerable numbers.) The larvæ, according to my observations, *may be either exposed or concealed;* the exposed ones are predominantly the older larvæ.

In one of the grasses (*Spartina michauxiana*) on which *Anaphothrips* was found in abundance at Douglas Lake, Michigan, the leaves bear on the upper surface a set of fine, but prominent, ridges running parallel to the axis of the leaf. Adult females and larvæ of *Anaphothrips* on the exposed parts of these leaves were always lodged between the tops of these ridges, and almost invariably *with their heads toward the base of the leaf.* If disturbed, they began to crawl along the crest of one of these ridges toward the base of the leaf. It was possible to force them to turn in the opposite direction, but if allowed to do so they soon turned again toward the base of the leaf, often continuing until they were among the rolled young leaves in the center of the top of the plant.

Anthothrips verbasci is found exclusively on one species of plant, the common mullein (*Verbascum thapsus*). Furthermore, it is rare that a specimen of mullein, of considerable size, is found free from the mullein thrips. Most of the thrips are found *among the florets or seed pods of the spike.* Less commonly they are to be seen on exposed surfaces, as on the leaves or stem lower on the plant; but *these exposed individuals are mostly adults.* The larvæ are usually hidden on the flower spike unless that situation is crowded by a large number of larvæ; and *the larvæ that are occasionally found exposed are mostly nearly fully grown.*

Anthothrips niger was not abundant enough during my stay at Douglas Lake that many observations of its

habitat and behavior could be made. One fact, however, is of interest in connection with an experiment to be described. While the adults live mostly on flowers, sometimes concealed, sometimes more or less exposed, the larvæ were always found concealed; moreover, *it was with difficulty that the larvæ could be driven from their retreat by pressing the flowers.* Frequently such vigorous squeezing was necessary to dislodge them that the larvæ emerging were injured; and a flower so treated was often found later to contain numerous dead larvæ. In this respect, the behavior of this species is in considerable contrast to that, for example, of *Euthrips tritici.*

The habitats and behavior described above can be "explained" in large measure if we say, as I at first proposed (1911), that certain species seek protection, or that certain other species have specific food requirements. Thus, it might be said that *Euthrips tritici* seeks safety in crevices, and flees danger when disturbed; that *Anaphothrips striatus* "prefers" grass for food, that it requires as much protection as its commissarial activities permit, and that its habitat and behavior are such as best fulfill these requirements. *Anthothrips verbasci* might be said to be limited to one article of diet, while protection is a minor matter.

This explanation might be acceptable as far as it goes, were it not that no species is immune to attack. I have seen larvæ of *Anthothrips verbasci* frequently captured by various bugs. Heads of mullein where thrips are found nearly always bear bugs of the family Capsidæ, and observations convince me that they prey almost wholly on the larvæ of the mullein thrips. The degree to which they check the thrips was tested experimentally as follows: Two mullein spikes of approximately equal size and equally infected with thrips were selected. The predatory bugs were removed from one of them, after which the spike was enclosed in a thin muslin bag. Two weeks later the bag was removed. The enclosed spike bore a large number of full-grown larvæ, a few had

pupated, and many were crawling on the inside of the bag. The spike that was exposed, on the other hand, bore but little over half the number of larvæ that were on the protected one, none were quite full grown, and none had pupated. Since nothing in the climatic conditions (heavy rains, for example) could have caused this difference, it is to be inferred that predatory bugs had devoured the larger larvæ in considerable numbers.

Yet *Anthothrips verbasci,* according to my earlier explanation, "chooses" its habitat almost exclusively in relation to food, protection being a minor consideration.

Can we not explain habitat and behavior in these insects in some way not implying choice, especially choice between conflicting preferences? May we not assume that certain elements of behavior are what they are without reference to their usefulness? If we grant the possibility of an affirmative answer to these questions, the experiments about to be described will have significance.

EXPERIMENTS ON BEHAVIOR

The following experiments were designed to show the reaction of the commoner species of Thysanoptera to what seemed to me the most probable external agents affecting their distribution and behavior, namely, light, contact and gravity. Inasmuch as I was not primarily interested in *how* a given reaction was brought about, but only in its end result, the experiments were rather crude. Refinements were unnecessary, and their omission enabled me to use much greater numbers of individuals than would otherwise have been possible. From ten to forty repetitions of each test were usually made. The experiments are described by species, only representative experiments being given.

Euthrips tritici

Light. Exp. 1.—Adults of this species were placed in a glass tube about three feet long and one inch in diameter, closed at the ends with corks. One end of the tube

was turned toward a small window, while the room was rather dimly lighted. All the thrips crawled rapidly toward the window. When the position of the tube was reversed, the thrips reversed their crawling, again going toward the window. The reaction was definite and invariable.

Exp. 3.—A close-fitting sleeve of black building paper was slipped over one half of the glass tube used in experiment 1. The thrips were collected at the exposed end by turning that end for a few minutes toward the window. The covered end of the tube was then turned toward the window. The thrips crawled rapidly toward the light, until they reached the shadow of the sleeve. Here they crawled about, apparently aimlessly, for half an hour an inch or two within the sleeve or just outside it.

Contact. Exp. 1.—When, in the light experiments, the tube was reversed in position as soon as the thrips reached one end, the insects immediately turned toward the opposite end. But if the tube was allowed to rest for some time, the thrips became settled quietly between the glass and the sloping surface of the cork. The tube could then be carefully reversed, and most of the thrips remained lodged between cork and glass for many minutes, some of them for hours. *The positive reaction to contact counteracted the positive reaction to light.*

Exp. 25.—A larva of this species was placed on a glass plate, upon which rested a microscope slide. When the larva in its crawling reached the slide, it came to rest in the angle formed by the glass plate and the edge of the slide. It remained there many minutes until disturbed.

Gravity. Exp. 17.—An adult female was placed in a glass tube which was enclosed in a black sleeve to exclude light, and the tube placed in a vertical position. The position of the thrips was marked with a wax pencil before putting on the sleeve. The sleeve was then removed momentarily at frequent intervals, and the position and direction of crawling of the insect noted. Most frequently it was found lower than the previous position,

and crawling downward. This was not always the case, however.

Of other specimens tried, some showed positive geotropism more definitely, some less definitely than the one described. None showed a negative reaction in the majority of cases.

Anaphothrips striatus

Light. Exps. 5 and 7.—Adults of this species were shaken out on a sheet of white paper near a window, and the course of their crawling was plotted as accurately as possible in my notes. Some individuals were decidedly negative to light, crawling directly away from the window every time they were tried, regardless of the direction in which they happened to be headed when they touched the paper. Others were indifferent to light, crawling in various directions. *Most of the males used were decidedly negative to light, females usually indifferent.*

Exp. 10.—Females taken from the exposed portions of leaves of *Spartina michauxiana,* and tested as above, were found in nearly every case to be *indifferent to light. Females from the curled young leaves of the same plants were as a rule negative to light.*

Exp. 6.—Larvæ were usually found indifferent to light, regardless of whether they came from exposed or concealed situations.

Exp. 15.—A single larva taken from the exposed part of a leaf, when placed in a glass tube one end of which was directed toward the window, crawled steadily toward the window. When the position of the tube was reversed, the larva at once reversed its direction. The tube was then placed in a black sleeve to exclude the light, and kept there for an hour. When it was removed, the larva showed for some minutes a *decidedly negative reaction to light.* Later, however, its behavior became indefinite, and *soon became markedly positive. Darkness had apparently temporarily reversed its reaction.*

Contact. Exp. 22.—A female of this species which was

negative to light was placed on a sheet of blotting paper. A small square of glass was placed over her, and supported at one edge, so that in crawling away from the window the thrips approached the edge of the glass which was in contact with the paper. She soon became lightly wedged between the glass and the blotter, and came to rest. Blotter, thrips and glass were then carefully turned through 180 degrees so that the negative reaction to light would have led the thrips out of its crevice; but she remained there for a long time. *Positive reaction to contact overcame the negative reaction to light.*

Another female, indifferent to light, was placed under a similar glass. In her random crawling she became wedged between the blotter and glass, and, notwithstanding that the blotter was occasionally turned in the meantime, *remained there several hours, until I lifted the glass.*

Another female, not negative to light, was placed under a similar glass square. She crawled from under it, but happened to crawl against the edge of the microscope slide that supported the glass cover. She settled quickly into the right angle formed by the slide and the blotter, and remained there a long time.

Gravity. Exp. 21.—A female which was indifferent to light was placed in a glass tube, and the tube set in a vertical position. The thrips immediately began to crawl downward. The tube was reversed, and the thrips immediately reversed its direction. A sleeve was placed over the tube to exclude the light, and frequently removed temporarily to observe the position of the thrips. In every case she was found crawling downward.

When the tube was held in an oblique position, the result was the same; the thrips crawled down the slope. If she was already crawling down, a slope of 5 to 10 degrees was found to be sufficient to keep her going in the same direction. But to reverse the direction of crawling, it was necessary to create a slope of about 45 degrees in the opposite direction. The same positive geotropism was shown when the thrips was placed on an inclined sheet of

paper; but being here at liberty to fly, she soon interrupted the experiment.

Numerous other females were tried, and all showed positive geotropism, some more promptly than others, but all perfectly definitely. A single male tested showed no definite reaction to gravity. A larva, nearly full grown, subjected to the same tests, showed as definite a positive reaction to gravity as did any of the females.

With the possible exception of the males, therefore, *Anaphothrips striatus is decidedly positive to gravity.*

Anthothrips verbasci

Light. Exp. 4.—Adults of this species, shaken out on a paper near a window, crawled in various directions. *None of them showed any definite reaction to light.*

Numerous larvæ, none of them over three fourths grown, *crawled directly away from the window in every instance.*

Exp. 12.—In this experiment adults from concealed places in mullein spikes were compared with those from exposed situations. They were shaken out on a sheet of paper near a window, and the direction of crawling noted. In every case, *those from concealed situations showed a fairly definite negative reaction to light.* Of those from exposed situations, *two were plainly negative, the remaining ten indifferent to light.*

Exp. 11.—Larvæ taken from concealment in a mullein spike were tested, on a sheet of paper, for their reaction to light. *Those of the smaller sizes crawled directly away from the window.* Those nearly full grown, while on the whole negative, crawled in a more or less devious path away from the window. One reddish larva, which from its color and size must have been *nearly ready to pupate, was especially indefinite in its reaction to light.*

Contact. Exp. 18.—Larvæ of various sizes, which were found to be negative to light, were placed on a blotter under a square of glass supported at one edge, as described for *Anaphothrips striatus.* When, in crawling

away from the window, they became wedged lightly between glass and blotter, and came to rest, the blotter with all on it was turned through 180 degrees. The larvæ turned their bodies so that their heads were directed away from the window, but did not crawl away. *The positive reaction to contact overcame the negative response to light.*

An adult tested in the same manner as the larvæ above described did not come to rest under the glass square. But happening to crawl against the microscope slide which supported the glass, the thrips came to rest in the right angle formed by the blotter and the edge of the slide, and remained there a long time.

Gravity. Exps. 13 and 20.—Adults and larvæ were put, one at a time, into a glass tube, which was set in a vertical position, and covered with a black sleeve to exclude light. Some were examined at frequent intervals, others were left half an hour without examination. In every case the thrips were found almost precisely where they were put at the beginning of the experiment. *This species is therefore indifferent to gravity.*

Anthothrips niger

Light. Exp. 2.—The red larvæ of this species were shaken out on a paper near a window, as described in other experiments. In every case the larva *crawled away from the window for a few seconds at first, then slowly turned toward the window, and continued indefinitely toward the light.* Once while the larva was crawling toward the light, I tapped the paper vigorously with a pencil, so that the thrips was lifted slightly from the paper and let drop; *it immediately reversed its direction, crawling from the window,* but in a few seconds turned again toward the light. The paper was jarred frequently, but always with the same result. To show whether the jarring made the response to light negative, or merely reversed whatever the larva was doing at the instant, the tapping was repeated at intervals of one or two seconds.

At the first tap, the larva, which had been crawling toward the window, immediately turned away from the light. Before it resumed its positive response to the light, the paper was tapped again; *the negative response continued.* In this way the larva could be kept crawling away from the light indefinitely. *Disturbance makes the reaction of the larva to light temporarily negative; otherwise it is positive.*

SUMMARY OF EXPERIMENTS

Euthrips tritici, when disturbed, is positively phototropic in both larval and adult stages. It is positively stereotropic, and the stereotropism is stronger than phototropism, at least under certain circumstances. Some individuals appear to be on the whole positively geotropic; others are indifferent.

Anaphothrips striatus.—Adult males are usually negatively phototropic. Females taken from exposed situations are usually indifferent to light, those from concealed situations usually negative. The larvæ are usually indifferent to light, regardless of the kind of place from which they are taken; a single larva that was positive was made negative by keeping it in the dark. Adults are positively stereotropic. The females and larvæ are positively geotropic.

Anthothrips verbasci.—Adults taken from concealed situations are usually negatively phototropic, those from exposed places tend to be indifferent to light. The larvæ are all negatively phototropic, except the full-grown ones, which may be indifferent. The larvæ are plainly positively stereotropic, the adults less plainly so, or not at all. Neither adult nor larva responds to gravity.

INTERPRETATION OF THE EXPERIMENTS IN THEIR RELATION TO DISTRIBUTION AND BEHAVIOR OF THRIPS IN NATURE

With the evidence from these experiments before us, may we not interpret the observed distribution and behavior of the Thysanoptera in nature somewhat as follows? Instead of explaining the fact that *Euthrips tritici*

always lives in concealed situations as due to a demand for protection, we may assume that it is due to the strong positive stereotropism of this species—aided in some cases by positive geotropism, where the flower inhabited is upright, but notwithstanding positive geotropism where the flower is inverted. The rapid escape by crawling or flight when disturbed is not due to the fact that this is the best way of avoiding danger, but to the positive reaction to light. Other species avoid danger by going deeper into crevices, because they are negatively responsive to light.

Anaphothrips striatus lives on grasses doubtless because it can not live on any other food, or because the reproductive processes are not stimulated by any other host plant. But their distribution and behavior on the grasses may be explained largely in terms of their reactions to the three agents tested in the experiments. The males usually live in concealed situations on the plants (curled-up leaves) because they are mostly negatively phototropic, and crawl down the leaves until they reach these concealed situations. Females may live either in exposed or in concealed places, for some of them are negative to light, others indifferent. The larvæ are either exposed or concealed, because they are indifferent to light. The eggs from which they hatch are probably laid by negatively phototropic females in the young curled leaves, and the leaves unfold as the larvæ develop; this explains why the exposed larvæ are much larger, on the average, than are those concealed in the young leaves. Perhaps the relation of cause and effect as here stated is reversed, at least for some cases. Concealment—*caused* in one way or another—may lead to negative phototropism, as in the larva which was made temporarily negatively phototropic by being kept in the dark.

The adults are lodged between the ridges on the upper side of the leaves of the grass *Spartina,* not for the sake of protection, it seems to me, but because they are positively stereotropic. Doubtless between the ridges is the

place where they can best suck the juices of the plant, but there is no need to assume that they deliberately choose this location in order to get their food most easily. Both adults and larvæ rest on these leaves with their heads directed toward the base of the leaf, and crawl toward the base of the leaf if disturbed, not because protection is most quickly to be found among the curled leaves at the center of the plant, but because the thrips are positively geotropic.

Anthothrips verbasci.—The larvæ of this species live hidden among the flowers of the mullein spike, not because they must get their food there, for they can get it from any part of the plant; nor do they hide there, it seems to me, to secure protection. They remain in these crevices because, excepting the largest larvæ, they are positively stereotropic and negatively phototropic. The adults are sometimes exposed, sometimes concealed, probably because in the former case they are usually indifferent to light, in the latter case negatively phototropic. (Or may they be made negative or indifferent according as they live—for one reason or another—concealed or exposed?)

Thus, while *Anthothrips verbasci* is limited to one food plant, and the food requirements are therefore probably exceedingly important, yet the distribution and behavior of the insects on this plant may be explained without appealing to anything like "choice" in other matters.

Regarding *Anthothrips niger,* I wish to call attention to but one fact. The difficulty with which the larvæ are driven forth from a flower in which they live appears to be due, not to a persistent attempt at concealment, but to the fact that on being disturbed they are temporarily negatively phototropic; if the disturbance is continued, the negative response continues.

The only argument which, it appears to me, could be advanced in favor of assuming that the Thysanoptera choose their locations, instead of adopting simple response to external stimuli as the correct explanation of

distribution, is the possibility that they have learned that certain modes of behavior are best suited (for example) to continued safety.

The reply to such an argument is first, that most of my studies on behavior have been made in an unsettled region, where the enemies of thrips incident to civilization are practically wanting, and where even the natural enemies are not abundant. It could hardly be assumed that every individual would learn to avoid its enemies in the course of its short lifetime, yet certain species seem to be invariable in their response to certain agents. Furthermore, many of the larvæ tested in the experiments could have been but a few days old. It is incredible that their reactions should have been, as in fact they were, as definite and invariable as those of older larvæ, if these responses were dependent on experience.

It seems to me, therefore, that the only satisfactory explanation of outdoor behavior and distribution of the Thysanoptera lies in the assumption that they are in large measure the result of responses to simple stimuli, and do not imply any degree of choice.

Origin and Adaptiveness of Responses to External Stimuli

The origin of such responses in Thysanoptera as have been described above is not, I believe, discoverable. Purposeful they most probably are not, as I have shown, if by purpose we mean conscious direction of actions to some end. But adaptive they no doubt are in many cases. Perhaps they are all adaptive, but I confess that my powers of analysis are not keen enough to prove such a view correct. That *Euthrips tritici* is positively phototropic when disturbed is no doubt the cause of frequent escapes from danger. One may even believe the *negative* phototropism of larvæ of *Anthothrips verbasci* to be adaptive, because they are much more sluggish than is *Euthrips tritici,* and could not escape quickly even if they should emerge into the light. They are probably safest,

therefore, if, when disturbed, they retire into still deeper crevices. But I am unable to discover the adaptiveness of the response of the larvæ of *Anthothrips niger* to light —at first negative, on being disturbed, but soon becoming positive. Nor can I understand why the males of *Anaphothrips striatus* are more definitely negative to light than are the females or larvæ. These reactions seem to me to be useless.

We need not demand that all of these responses be adaptive, any more than that they be purposeful. Responses have arisen, no one knows how. They have been preserved, and we can but speculate as to the method of their preservation. Natural selection may be responsible for the preservation of the useful, and it may have eliminated responses that were harmful. But other responses of no value whatever, but likewise harmless, may have been allowed to persist, without help or hindrance from selection.

(To be continued.)

SHORTER ARTICLES AND CORRESPONDENCE

THE ENDEMIC MAMMALS OF THE BRITISH ISLANDS

WHEN, in 1891, I was collecting information to be used by Dr. A. R. Wallace in preparing the second edition of his "Island Life," I found much skepticism among naturalists concerning the alleged endemic or precinctive elements of the British fauna. Dr. Wallace was able to give lists of supposed precinctive species and varieties belonging to several groups, but for the mammals he was obliged to state, "it is the opinion of the best authorities that we possess neither a distinct species nor distinguishable variety." We little imagined that about twenty years later the British Museum would issue a work describing ten species and twenty subspecies of mammals peculiar to the British Islands; twenty-one of these being actually undescribed at the time I made my enquiries, and the rest then reposing quietly in the synonymy. Still less did we imagine that such a revision, when made, would be the work of an American, coming over from the United States National Museum to show Europeans the neglected wonders of their own fauna! The Catalogue of the Mammals of Western Europe, by Mr. G. S. Miller, published last year by the British Museum, is certainly one of the most remarkable zoological works ever produced, and is well worthy of the attention of all naturalists, whether specially interested in the Mammalia or not. While so many students of genetics are giving us the results of their experiments in breeding mammals, it is worth while to turn also to the results of nature's long-time breeding experiments, so clearly set forth by Mr. Miller in the volume cited. What, after all, is the connection between the phenomena seen by the breeder and the facts of mammalian evolution? Do species and subspecies differ by "units," and do the variations observed in captivity correspond in any way to the recorded specific and subspecific differences?

A complete analysis of Mr. Miller's volume can not be made at the present time, but I have extracted the list, given below, of the forms supposed to be confined to the British Islands, giving their distribution and principal distinctive characters. I have added to Mr. Miller's list three quite recently described animals. On examining the list, it appears that a few of the species must belong to the older fauna of the country, not wholly exterminated by the glacial ice and periods of partial submergence. Such are

Mustela hibernica of Ireland and *Microtus orcadensis* of the Orkney Islands. It is at least suggestive, in this connection, that so many of the Scottish islands yield animals differing from those of the mainland. In the majority of cases, however, the peculiar British mammals are closely related to those of the continent, and might well be of very recent origin. There is a decided tendency to darker colors, such as has been noted also among British moths. In spite of this tendency, however, some forms are lighter than their relatives, the most conspicuous case being the light-tailed British squirrel. In several cases the difference noted has in part to do with particular phases; thus the squirrel has no dark phase, and the ermine does not turn so white in winter. The British red grouse, it will be remembered, is peculiar in lacking a white winter phase. Some of these differences may be due to the direct effect of the mild and moist British climate, and would perhaps disappear in the descendants of British animals taken elsewhere. The experiments on birds by Beebe are very suggestive in this connection. In other cases, the distinctions are such as might readily result from changes in one or two "units," such as are observed in experimental breeding. When we have a variable type, subject to losses and new combinations of unit characters, it is perhaps to be expected that different groups of individuals, isolated from one another, will after a time produce different homozygous combinations. That is to say, the result comes from a long series of "accidents," which will probably not be duplicated in two different places. In this way mere isolation may be an adequate cause of modification, providing always that through variation degrees of heterozygosity have arisen.

In the common house mouse, *Mus musculus,* Hagedoorn[1] has isolated and figured a great number of color varieties, for nearly all of which he has constructed zygotic formulæ. Little[2] has also described and figured a similar series of varieties, apparently in ignorance of Hagedoorn's paper, which he does not cite. He gives zygotic formulæ for thirty-two different varieties, but not all of them are visibly different. Albino varieties, resulting from the dropping out of a particular determiner, may be produced, corresponding in other respects to each of the thirty-two colored forms, although they all look alike, and will only show their true characters on crossing. Several of the varieties show

[1] *Zeit. f. ind. Abst. Ver.*, 1912.

[2] "Experimental Studies of the Inheritance of Color in Mice," 1913.

noteworthy fluctuating variability, due to differences in expression.

Mus musculus, then, is very conspicuously variable in color; yet Miller's book records only one subspecies, that of the Mediterranean region and the Azores, which is less dusky and more yellowish, with the under parts buffy grayish. It possibly agrees with Little's "dilute black agouti" variety. On the other hand, *M. musculus* has a recognized subspecies in Mexico, where it must have developed since the species was introduced by man. The mice of St. Kilda and the Faroe Islands, although given as distinct species, are derivatives of *Mus musculus,* differing in other points than color. In connection with subspecific differences in size, Sumner's experiments with different temperatures should be noted, since they prove that differences of temperature might lead to readily measurable differences in dimensions, wholly unconnected with losses of determiners or new zygotic combinations. Whether or not diverse conditions of this sort would ultimately affect the germ plasm, their effects would be patent long before and quite independently of any such modification. On the whole, the poverty of *Mus musculus* in subspecies would suggest that the variations observed by breeders are not, as a rule, the stuff that new subspecies are made of. Against this argument may well be adduced the fact that *M. musculus* is an urban animal, constantly traveling about, so that incipient races do not remain isolated. Here the closely related rats, *Epimys,* are worth considering. For Europe Miller can only recognize the Norway, Black and Alexandrian rats, all widespread, practically cosmopolitan. Yet in the Malay Archipelago, where *Epimys* is distributed over myriads of islands, large and small, the species are innumerable. One can almost take a map and indicate where new species of *Epimys* are to be found, namely, on those islands still unexplored. Years ago, when the writer was actively engaged in studying the British Mollusca and Lepidoptera, the question of endemic forms was constantly in mind; but in those days we failed to discriminate properly between the different classes of "varieties." We made the mistake of looking for well-marked "sports" or aberrations, rather than for constant but only slightly distinguished local races. There was a practical reason for this, in the fact that by searching the literature we could ascertain whether a well-marked variation had been reported from the continent; whereas the determination of subspecific types analogous to those described by Miller among

mammals required long series from different parts of Europe, and these we did not possess, and could not readily obtain. Miller, following the custom of mammalogists, lays great stress on subspecies, but almost ignores individual variations, except such as are expressed by the statistical data regarding size. By reading the synonymy, one can see that many such variations have received names, and I can not doubt that the time will come when these names will be generally used. In this case, it will be extremely desirable to use the same adjectival name for analogous varieties of different species, and beyond the limits of subspecies it ought not to be held that a name once used in a genus can not be employed again. It may be true that most or all of the "individual" varieties can be expressed by zygotic formulæ, but one can not remember all these formulæ, nor use them in speech with any comfort. Moreover, they have to do with the germinal constitution rather than the patent characters. Little provides all his varieties with polynomial English appellations, but would not Latin varietal names be better? Following his theory concerning the pigments, some of the varieties receive names which do not suggest the animals at all; thus "brown-eyed yellow," according to the apparently excellent colored plate, is light orange-ferruginous, while "sooty-yellow" is dark gray with yellowish under parts. Morgan[3] describes a wild variety of *M. musculus* from Colorado, which he calls "mauve," but from the detailed account it is rather "fauve," namely, fulvous or yellowish brown. It must be similar to the Old World subspecies *azoricus,* or possibly that subspecies introduced? If we had standard scientific names for the different forms, we should try to compare our specimens with the types or descriptions of those names, and it would not be left to authors to use such miscellaneous descriptive terms as might occur to them. For *Mus musculus,* possibly Little's apparently excellent colored plates might be made the standards for a series of names. Thus his Fig. 9 (pl. 3) is the animal named *niger* as long ago as 1801; Fig. 10, the dilute black, would naturally take the name *nigrescens.* Fig. 12 is probably *albicans* of Billberg, 1827.

MAMMALS PECULIAR TO THE BRITISH ISLANDS

Insectivora

Sorex araneus castaneus (Jenyns 1838). Great Britain. Not so dark as true *araneus.*

[3] *Ann. N. Y. Acad. Sci.,* XXI, p. 106.

Sorex granti (Barrett-Hamilton and Hinton 1913). Inner Hebrides. Differs from *araneus* by the contrast between bright-colored flanks and dusky upper parts; teeth also different.

Neomys fodiens bicolor (Shaw 1791). Great Britain. Under parts usually washed with wood-brown instead of buffy whitish; skull smaller.

Chiroptera

Rhinolophus ferrum-equinum insulanus Barrett-Hamilton 1910. Central and S. England. Wing shorter.

Rhinolophus hipposideros minutus (Montagu 1808). England and Ireland. Wing shorter.

Carnivora

Mustela erminea stabilis (Barrett-Hamilton 1904). Mainland of Great Britain. Rather large, with large teeth; color somewhat different, a little darker above. Change to white in winter less complete and regular than in continental forms.

Mustela erminea ricinæ (Miller 1907). Islands of Islay and Jura, Scotland. Smaller than *stabilis;* proportions of skull different.

Mustela hibernica (Thomas and Barrett-Hamilton 1895). Ireland and Isle of Man. Quite distinct; recognized by combination of black-tipped, heavily penciled tail with entirely dark ear and upper lip. Superficially like certain North American forms.

Felis sylvestris grampia (Miller 1907). Scotland; formerly throughout Great Britain. Darker, with more pronounced black markings.

Rodentia

Lepus europæus occidentalis de Winton 1898. England, Scotland and Isle of Man. Buffy tints rich and dark.

Lepus timidus scoticus (Hilzheimer 1906). Highlands of Scotland. Smaller; rarely becomes so white in winter as Alpine race.

Lepus hibernicus Bell 1837. Ireland. Distinguished by the strongly russet color and partial or complete absence of white winter coat. Larger than *scoticus.*

Evotomys alstoni Barrett-Hamilton and Hinton 1913. Island of Mull, Hebrides.

Evotomys glareolus britannicus (Miller 1900). Great Britain. Smaller; color less intense.

Evotomys skomerensis Barrett-Hamilton 1903. Skomer Island, off coast of Wales. Color above unusually light and bright; skull peculiar.

Microtus agrestis exsul Miller 1908. North and South Uist, Hebrides. Resembles true *agrestis* of Scandinavia; teeth peculiar, a character usually present which elsewhere in the species occurs as a rather rare anomaly.

Microtus agrestis macgillivraii Barrett-Hamilton and Hinton 1913. Island of Islay, Hebrides.

Microtus agrestis hirtus (Bellamy 1839). England and South Scotland. Smaller than typical *agrestis;* upper parts noticeably tinged with russet, and venter washed with wood-brown.

Microtus agrestis neglectus (Jenyns 1841). Highlands of Scotland. Not so small as *hirtus;* upper parts darker.

Microtus orcadensis Millais 1904. South Orkney Islands. Related to *M. sarnius* of Guernsey and the Pleistocene *M. corneri* of South England. Distinguished by its large size and dark color.

Microtus sandayensis (Millais 1905). Sanday Island, N. Orkney group. Allied to *orcadensis,* but skull differing; upper parts much lighter.

Microtus sandayensis westræ Miller 1908. Westray Island, N. Orkney group. Not so pale as in typical form; teeth differing a little.

Arvicola amphibius (L. 1758). Typical subspecies. England and South Scotland. Large; color moderately dark.

Arvicola amphibius ater (Macgillivray 1832) = *reta* Miller 1910. Scotland, except southward. Darker, melanism frequent. The name was changed on account of *Hypudæus terrestris* var. *ater* Billberg 1827, but the change is perhaps needless, as Billberg's animal was not a subspecies, and has not been treated as a species or subspecies under *Arvicola.*

Apodemus hebridensis (de Winton 1895). Lewis and Barra islands, Hebrides. Large, with small ears; color dark.

Apodemus hirtensis (Barrett-Hamilton 1899). Island of St. Kilda. Near *hebridensis,* but skull larger and color darker.

Apodemus fridariensis (Kinnear 1906). Fair Isle, Shetland group. Large; skull peculiar; colors also somewhat peculiar.

Apodemus flavicollis wintoni (Barrett-Hamilton 1900). England. Under parts with duller color, pectoral spot more diffuse.

Mus muralis Barrett-Hamilton 1899. Island of St. Kilda. Like *M. musculus* but feet and tail less slender; skull peculiar.

Mus fœroensis (Clarke 1904). Faroe Islands. Larger than *musculus* and *muralis;* hind foot very robust; tail thickened.

Sciurus vulgaris leucourus Kerr 1792. Great Britain and Ireland. Small; tail drab, fading in summer to cream buff. No dark phase.

Ungulata

Cervus elaphus scoticus Lönnberg 1906. Great Britain. Color darker and less gray than in the related Norwegian form.

Capreolus capreolus thotti Lönnberg 1910. Great Britain. Darker, face darker than body.

I thought it of interest to compare the above British list with a similar one for the Spanish peninsula (Spain and Portugal). The latter area is continuous northward with France, but the Pyrenees constitute a barrier. The Iberian peninsula differs so much in its recent geological history from Britain, and is at the same time so much more southern, that we should expect to find the faunal elements very different. This expectation is realized, yet the difference in numbers between the two lists is not very great, and the number of Iberian forms treated as distinct *species* is exactly the same (12) as that for the British Islands. This suprising result is evidently due to the numerous small

islands of the British group, such islands being wanting around the coasts of Spain.

MAMMALS PECULIAR TO THE SPANISH (IBERIAN) PENINSULA

Insectivora

Talpa occidentalis (Cabr.).
Galemys pyrenaicus rufulus (Graells.).
Sorex araneus granarius Miller.
Neomys anomalus Cabr.
Crocidura mimula cantabra (Cabr.).
Crocidura russula cintræ Miller.
Erinaceus europæus hispanicus B.-Ham.

Chiroptera

(None.)

Carnivora

Canis lupus signatus Cabr.
Canis lupus deitanus Cabr.
Meles meles marianensis (Graells.).
Martes foina mediterranea (B.-Ham.).
Mustela nivalis iberica (B.-Ham.). (Also Balearic Is.).
Mustela putorius aureolus (B.-Ham.).
Mungos widdringtonii (Gray).
Genetta genetta (L.), typical subsp.
Felis sylvestris tartessia (Miller).
Lynx pardellus Miller.

Rodentia

Lepus granatensis Rosenb. (Also Balearic Is.).
Lepus granatensis gallæcius Miller.
Eliomys lusitanicus (Reuvens).
Glis glis pyrenaicus Cabr.
Microtus agrestis rozianus (Bocage).
Microtus asturianus Miller.
Arvicola sapidus Miller, typical subsp.
Pitymys lusitanicus (Gerbe).
Pitymys mariæ (Major).
Pitymys pelandonius Miller.
Pitymys depressus Miller.
Pitymys ibericus (Gerbe), typical subsp.
Pitymys ibericus centralis Miller.
Pitymys ibericus pascuus Miller.
Pitymys ibericus regulus Miller.
Mus spicilegus hispanicus Miller.
Mus spicilegus hispanicus Miller.
Sciurus vulgaris numantius Miller.
Sciurus vulgaris infuscatus (Cabr.).
Sciurus vulgaris seguræ Miller.
Sciurus vulgaris bæticus (Cabr.).

Ungulata

Sus scrofa castilianus Thomas.
Sus scrofa bæticus Thomas.
Cervus elaphus hispanicus Hilzh.
Capreolus capreolus canus Miller.
Capra pyrenaica lusitanica (França).
Capra pyrenaica victoriæ Cabr.
Capra pyrenaica hispanica (Schimp.).
Rupicapra parva (Cabr.).

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NOTES AND LITERATURE

SWINGLE[1] ON VARIATION IN F_1 CITRUS HYBRIDS AND THE THEORY OF ZYGOTAXIS

SWINGLE in two recent papers has published some very interesting observations on *Citrus* species and their F_1 hybrids. On the basis of these observations, the somewhat startling statement is made that current theories of heredity and variation give no adequate explanation of variability in F_1 hybrid generations from "pure bred" parent strains. Swingle assumes this variability to be so great that qualitative differences in chromosomes can not account for it. As the chromosomes in the F_1 hybrid remain unfused until synapsis, there is said to be no opportunity for quantitative exchange of hereditary substance, so that this variation can not be accounted for on this basis. Hence,

> if proof can be given to show that in certain specific cases, pairs of gametes of *identical hereditary composition*[2] give rise to very diverse organisms, the way has been opened for a general reinvestigation of the validity of our modern theories of heredity.

The term "pure bred" as used by Swingle implies that certain *Citrus* species reproduce themselves in a relatively faithful manner from seed, there being no overlapping of distinguishing specific characters and very little variation of these characters intraspecifically. *C. aurantium* and *C. trifoliata* are examples of such widely separated species. The former has been grown from seed in Florida for two hundred years, and though variations have appeared, they are said to differ but little from the general type of *C. aurantium,* and in no way to approximate that of *C. trifoliata.*

On the basis of evidence of this kind, Swingle believes the various *Citrus* species (*C. aurantium, C. trifoliata, C. medica limonum,* etc.) breed true in nearly all their characters and especially in those which differentiate them from one another. Hence, for genetic studies, the germ cells of these species are

[1] Swingle, W. T., "Variation in First Generation Hybrids (Imperfect Dominance): Its Possible Explanation through Zygotaxis," IV° Conf. Internat. de Genetique, Paris, 1911, pp. 381–394; "Some New Citrus Fruits," *Amer. Breed. Mag.,* 4: 83–95, 1913.

[2] The italics are my own.

assumed, in respect to these differential characters, to be pure; or, expressed in more technical language, each species is for the characters under observation, genotypically homozygous. This assumption is based on wholly inadequate evidence, as will be shown later.

Citrus trifoliata crossed with other *Citrus* species (*C. aurantium*, etc.) gave F_1 hybrid families showing a large degree of variability, even when the seeds from a single cross having identical male and female parents were grown. This variability expressed itself in foliage, habit of growth, and fruit, and was especially noticeable in the latter, the fruits of the F_1 individuals showing differences in color, size, texture, shape, number of seeds, and flavor. For example, from a single cross of *C. trifoliata* × *C. aurantium*, the 11 resulting hybrid seeds gave rise to F_1 plants (citranges) differing in foliage, habit of growth, and very strikingly in fruit. The fruit of one of these citranges, the "Morton," was smooth, round, very large, and orange-colored; those of the "Colman" were rather flattened, globose, pubescent, yellow, almost seedless, and lacked the disagreeable oil common to the others; while those of still another type, the "Willits," were often monstrously fingered. The "Phelps" was bitter, while the "Saunders" almost lacked this quality. The "Rustic" often has double fruits with many seeds, and a habit of growth more like its *aurantium* parent.

When varieties of the lemon were crossed with *C. trifoliata*, still greater differences in the F_1 generation (citremons) resulted. These consisted largely of "abnormal" foliage developments. Hypophylls, though absent in the common *Citrus* species are extremely characteristic of *C. trifoliata*. About 20 per cent. of the lemon-trifoliata hybrids developed an intensified form of this character, and this proportion occurred in each case in crosses involving three different varieties of lemon. The tangerine orange × grape fruit (tangelo) in the F_1 generation was almost as variable as the citrange families. F_1 hybrids between the West Indian lime and the kumquat (limequat) were strikingly different in such characters as aroma, flavor, acidity of pulp and thickness of skin.

Although much stress has been laid on the differences in these F_1 hybrids, there were numerous similarities. For example, all the *Citrus* hybrids involving *C. trifoliata* in their parentage have compound, semi-evergreen leaves, increased hardiness and fruits

with abundant bitterish, acid juice. Two of the citranges (Colman and Cunningham) have the pubescent fruit character of *C. trifoliata,* while the others are smooth-skinned.

The author's data led him to formulate in substance the following conclusions, which I have grouped and stated in my own language.

1. *Citrus* species are but slightly variable in the characters which differentiate them, and, in the sense that no overlapping takes place, may be said to breed true, their germ cells being genetically pure for these differential characters.

2. Individual plants of the F_1 hybrid generations between these species are strikingly variable, although all are, in a given cross, the zygotic product of *pairs of gametes* of *"identical hereditary composition."*

3. Modern theories of heredity can not account for this variation.

These are not the conclusions, however, in which all present-day geneticists would concur. In the first place, few "modern" geneticists would take Swingle's view concerning the "pure breeding" ability of the various *Citrus* species, nor even of *C. aurantium.* Webber, in the Encyclopedia of American Horticulture, notes that 70 varieties of the common sweet orange are grown within our borders, and although a few varieties are fairly constant, the majority of these do not breed true from seed. Practically the same idea has been gained by certain prominent taxonomists of the genus *Citrus.* De Candolle specifically calls attention to the remarkable variability of the whole group; and Professor Hume of Florida remarks on the same fact in certain Experiment Station publications. As to the variability among the individuals in the special strains used by Swingle in his breeding work, no data are given, so that it can not be affirmed that inbred progeny from them would have been duplicates as far as hereditary characters are concerned. *Citrus* plants naturally cross fertilize, and from this cause alone no dependence can be placed on their ability to produce progeny, which are exact duplicates of themselves when inbred; in fact, the inference is that they would not. Hence, as far as intraspecific constancy of hereditary characters is concerned, Swingle's statement can not be accepted until more exact information is produced.

Swingle says no interspecific gradations occur between these various species, especially *C. trifoliata* and *C. aurantium.* Grant-

ing this, the two species have clearcut differences in leaves (evergreen or deciduous, unifoliolate or compound), in resistance to cold (difference in ability to withstand certain degrees of temperature) and in numerous fruit characters (presence or absence of pubescence, quality of juice, quantity of seed, size of fruit, etc.).

From the standpoint of modern theories of heredity as regards variation in F_1 hybrid generations, it matters little whether so-called species intergrade or whether their differences are clear-cut and all variation is intraspecific. In either case, if crosses were made, variation among the F_1 individuals from a single family might or might not occur. In either case, no violence to modern theories of heredity would result and no new problems would arise. But if two species that differ from each other in part or all of their characters, but breed true intra-specifically (genotypically homozygous) are crossed, and F_1 variation results, then modern theories of heredity would be compelled to change front and invoke the aid of new hypotheses. Swingle's data, assuming that intraspecific variation in *Citrus* species occurs, does not present a problem of this kind at all. *C. aurantium* and *C. trifoliata* each possess distinctive characters, but convincing data are not at hand to warrant any belief in the homozygosity of these differential characters or of even those the two species may have in common. The evidence directly, and one might almost say conclusively, opposes such a conclusion. If these species are not homozygous in all of their characters, then one can not affirm, in the light of modern theories, that all the gametes produced by a particular group of individuals called a species are identical in hereditary composition, nor even that the gametes of one individual of such a species are identical as to hereditary potentialities. At the risk of wasting valuable space by repeating what is extremely common knowledge to genetic students, let us assume, for the purpose of argument, that *C. aurantium* and *C. trifoliata* are homozygous in all their respective characters except one. In the former, the character *A* is heterozygous and peculiar to this species. Likewise, in *C. trifoliata, B* is heterozygous and differential. All the remaining characters of the two species may be symbolized, respectively, by the formulæ *XX* and *YY*. When *XXAabb* (*C. aurantium*) is crossed with *YYaaBd* (*C. trifoliata*), the resulting progeny would appear in the approximate proportion of $1\,XYAaBb : 1\,XYAabb : 1\,XYaaBb : 1\,XYaabb$, providing

A and *B* are single factor characters. In the majority of characters, the F_1 hybrids would be intermediate or possess those of either one or the other parent, since all the F_1 individuals would be alike as far as any hereditary quality symbolized by *XY* is concerned, providing the plants were all grown under the same environmental conditions. But these F_1 individuals would not be alike as regards the inheritance of the characters *A* and *B*. Experimental evidence from crosses of this kind show us that four different F_1 forms may result, the distinctions between them arising from the presence or absence, through inheritance, of the characters *A* and *B*. Dominance is assumed to be absent in this illustration.

Swingle's *Citrus* hybrids, though involving greater complexity because a large number of parental characters instead of two are probably heterozygous, are of the same general type as those of the illustration and lend themselves to the same interpretation. Owing to the absence of sufficient exact experimental data, one can not speak of unit characters and factors in these hybrids, but one may say without violence to modern theories of heredity that one or both of the parents involved in the crosses which produced the Colman and the Cunningham were heterozygous in the factors or factor for pubescence, that various size factors were heterozygous and that one parent was homozygous for absence and one for presence of the factors for hardiness, compound leaves and evergreen foliage.

F_1 variation in *Citrus* hybrids then, in the light of the data at hand, apparently results from differences in the gametic composition of the heterozygous parents.

Swingle calls attention to other cases of variation in F_1 hybrids from two pure stocks which support his contention that this phenomenon of F_1 variation is very general, though usually obscured through variation due to heterozygous parent stock. Collins and Kempton[3] crossed a race of corn breeding true to waxy endosperm with one constant for horny endosperm. Horny endosperm was dominant in F_1 and the F_2 generation segregated in the expected ratio of 1 waxy to 3 horny kernels. This ratio represented the average proportion of each when the ears of all the plants were lumped together. The F_2 progeny of each selfed

[3] Collins, G. N., and Kempton, J., II, 1912, "Inheritance of Waxy Endosperm in Hybrids of Chinese Corn," IV° Conf. Internat. de Genetique, 1911, p. 347; also Circ. No. 120, Bur. of P. I., U. S. Dept. of Agr., 1913.

F_1 plant when taken by itself gave some ears as low as 13.7 per cent. waxy, while others exceeded the expected proportions and gave ears as high as 33.3 per cent. waxy. The investigators point out that this variation is not the result of the laws of chance as the deviation is far greater in many cases than the probable error. Therefore, says Swingle,

> there can be no doubt but that their varying percentages represented real differences in the hereditary composition of the first generation plants. It would be hard to find a more conclusive case since there could be no doubt as to the purity of the parents and what is more rare no possible doubt as to whether a given kernel had a waxy or a horny endosperm.

Mendelians are said to be unaware how fatal this phenomena is to some of the chief tenets of modern theories of heredity, and they are also accused, somewhat unjustly, I believe, of applying the term "imperfect dominance" to this and to the *Citrus* phenomena.

In this case, both parents were undoubtedly homozygous for their respective endosperm characters, so that heterozygosity will not account satisfactorily for the deviations. But this is a different phenomena than Swingle found in his *Citrus* hybrids, for here one is dealing with a fluctuation in a proportion or ratio involving the same character, while in his experiments the difficulty was the variation in presence and absence of distinct and often new characters, indicating an extremely heterozygous parentage.

As an explanation or working hypothesis for his own and similar data, Swingle advances a somewhat new and suggestive chromosome theory on the assumption that it fills an urgent need. The theory of zygotaxis, as it is called, may be summarized as follows:

Maternal and paternal chromosomes probably persist side by side in the cells, unchanged in quality and number throughout the whole development of the F_1 organism. This being true, Swingle, in order to explain his data, assumes that the influence in character formation exerted by chromosomes on the F_1 hybrids, is in some cases due to their relative positions in the nucleus, and that these relative positions result from accident or at least are determined at the moment of nuclear fusion in fertilization, and remain unchanged in succeeding cell generations. He further

assumes that those chromosomes lying nearest the nuclear wall (peripheral) are better nourished than those centrally located, and hence they exert more influence in character formation, and dominating synapsis, produce gametes similar in their hereditary character to the cells of the first generation hybrids, whose character in turn was determined at fertilization by the configuration the chromosomes took in the fusion nucleus. On this theory, reversions, sports, etc., may result from sudden changes in the nuclear configuration.

Three types of nuclear configuration are assumed to occur in higher organisms, the character and effects of which are synoptically outlined below.

1. *Interspecific Hybrids.*—Usually sterile and intermediate. Chromosomes repel each other and occupy opposite sides of the F_1 zygote nuclei, exerting equal influence in the ontogeny of F_1 organisms, explaining why first generation hybrids of this character are always intermediate, little variable and usually sterile. Synapsis often impossible.

2. *Mendelian Crosses.*—Abnormally inbred races of domesticated animals and plants. F_1 generation usually intermediate, fertile, dialytic at synapsis. Dominance of certain characters in these hybrids is due to the inherited potentialities of the chromosomes rather than to their nuclear positions.

3. *Normal Cross-bred Species.*—Probably normal in wild species. Hybrids usually vigorous, fertile, and variable. Free intermingling of chromosomes in the fusion nucleus at fertilization. Nuclear configuration permanent for each individual. Synapsis normal.

This elaborate and attractive theory, based admittedly to a great degree on assumptions, is advanced by Swingle in the belief that it will help to clarify the problems of heredity, even though he acknowledges it does not help one to arrive at satisfactory explanations. In the reviewer's opinion, however, the field of genetics is already burdened with enough theories of this particular type and the somewhat unnecessary but ever-increasing new additions serve to confuse rather than clarify the ideas of the average student of genetics. Besides, Swingle's assumption that maternal and paternal chromosomes in the cells of F_1 hybrids repel each other and do not mingle in the F_1 zygote cells is not borne out by the few cytological facts at our command. Rosen-

berg's[3] work on species hybrids of *Drosera,* Moenkhaus's[4] investigations of species hybrids in fish and some work on certain hybrids in the Echinodermata group give us facts that directly oppose such an assumption. As a further criticism, one may say that most biologists who have had experience with pedigree cultures would decidedly criticize the synoptic outline and the narrow sphere assigned to Mendelian phenomena.

Aside from the theoretical considerations, these two papers contain descriptions of *Citrus*-like species new to occidental horticulture, together with a somewhat detailed account of the various *Citrus* hybrids and their hardiness and practical value, showing the truly fine results achieved by the workers in this field toward moving the *Citrus* belt northward and adding *new* varieties of this genus to the world's horticulture.

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BROOKLYN BOTANIC GARDEN,
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[3] Rosenberg, O., "Cytologische und Morphologische Studien an *Drosera longifolia* × *D. rotundifolia,*" Kungl. Svenska Vetenskapsakademiens Handlinger., 43, N: ou, pp. 1–64, 1909. 4 Tafn.

[4] Moenkhaus, W. J., "The Development of the Hybrids between *Fundulus heteroclitus* and *Menidia notata* with especial reference to the Behavior of the Maternal and Paternal Chromatin," *Amer. Jour. of Anatomy,* 3: 29–65, 1904. Plates I–IV.